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The air chambers of Grimaldia fragrans *

ALEXANDER W. EVANS

(WITH FOURTEEN TEXT FIGURES)

INTRODUCTION

In most of the Marchantiales the thallus shows a layer of green tissue with air spaces or chambers below the dorsal epidermis. These chambers exhibit many differences when the group as a whole is considered, but it is possible to refer the majority to three distinct types. To these the names of the representative genera *Riccia*, *Reboulia* and *Marchantia* may be applied.

In the *Riccia* type the chambers occupy a single layer and are in the form of canals with their long axes approximately vertical; the canals are usually narrow and bounded by only four rows of cells, but in certain cases they are broader and bounded by a greater number of cells. In the *Reboulia* type the chambers are in two or more layers (at least in the median portion of the thallus) and are in the form of irregular polyhedrons, often tending to be isodiametric; this type is sometimes complicated by cellular outgrowths into the chambers. In the *Marchantia* type the chambers are again in a single layer (as in the *Riccia* type) but are in the form of more or less flattened polygonal prisms with their longer dimensions approximately horizontal; they are further distinguished by the presence of numerous simple or branched green filaments, extending from the floors of the chambers nearly or quite to the epidermis. In all three types the chambers communicate with the outside air by means of openings in the epidermis. In the *Riccia* type these may be nothing more than continuations of the canalicular chambers, but in the two other types the openings are usually surrounded by specialized epidermal cells and form the characteristic air pores or epidermal pores of the group.

Among North American genera the *Riccia* type is restricted to *Riccia* and *Oxymitra;* the *Reboulia* type is found in *Ricciella*,

* Contribution from the Osborn Botanical Laboratory.

Ricciocarpus, *Peltolepis*, *Sauteria*, *Clevea*, *Plagiochasma*, *Reboulia*, *Grimaldia*, *Neesiella*, *Cryptomitrium*, *Asterella* and *Bucegia;* while the *Marchantia* type occurs in *Corsinia*, *Targionia*, *Conocephalum*, *Lunularia*, *Preissia* and *Marchantia*. The reduced air chambers of *Cyathodium* conform best perhaps to the *Marchantia* type, in spite of the absence of green filaments, while the adult thallus of *Dumortiera* lacks air chambers altogether.

The genus *Grimaldia* Raddi, as understood by most recent writers, contains about half a dozen species. The most widely distributed of these is *G. fragrans* (Balb.) Corda, which is found in Europe, Asia and North America. Other well-known species, closely related to *G. fragrans*, are the Mediterranean *G. dichotoma* Raddi and the Californian *G. californica* Gottsche. In the eastern parts of the United States *G. fragrans* is sometimes locally abundant, preferring sunny trap ridges and growing on earth among rocks, rather than on the rocks themselves. It was in such a locality as this, on West Rock Ridge, near New Haven, Connecticut, that the material used in the present study was collected. The narrow thallus is firm and compact and produces an abundance of purple ventral scales with bleached-out appendages. The upper surface is grayish green and shows no indications of the boundaries of the air chambers beneath the epidermis. The margins, as well as the ventral surface, are more or less pigmented with purple. The species is markedly xerophytic, the margins becoming involute when dry, thus covering over and protecting the upper surface.

THE AIR CHAMBERS OF THE MATURE THALLUS

The green tissue of the thallus in *Grimaldia* has been repeatedly described, most of the observations having been based on either *G. fragrans* or *G. dichotoma*. Unfortunately the descriptions show marked discrepancies. Stephani (11), for example, states that the air chambers are densely filled with erect green filaments composed of long cylindrical cells, and K. Müller (6, p. 259) notes the presence of vertical plates of cells in addition to the filaments. Schiffner (9, p. 309) criticizes these descriptions. According to his account the chambers of *Grimaldia* undergo a secondary partitioning by means of irregular green lamellae which

grow upward from the floors and lateral walls of the chambers. A spongy tissue is thus formed in which narrow air spaces run, scarcely broader than the thickness of the lamellae, and the original partitions of the chambers soon become unrecognizable. He admits that in section the plates of cells one cell thick look like filaments and that marginal cells of the plates sometimes project as teeth, but he maintains that actual filaments are never present and that this fact is at once made evident by sections of the green tissue cut parallel with the surface of the thallus. Massalongo (5, p. 730), on the other hand, agrees with Stephani and states that the chambers are filled with vertical uniseriate filaments, some of

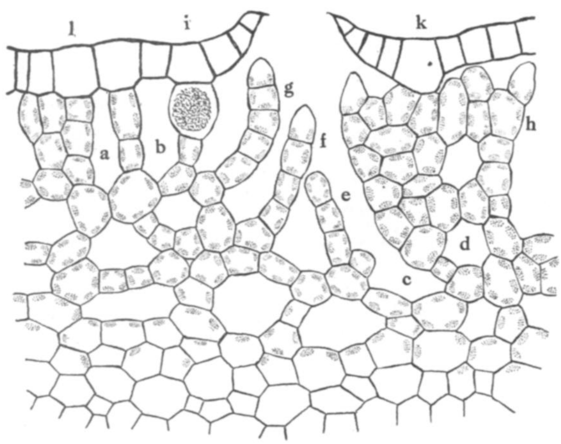


FIG. 1. Transverse section through epidermis and green tissue, × 270. *a–d*, air chambers; *e–g*, apparent filaments; *h*, plate-like outgrowth; *i*, *k*, *l*, boundaries between chambers.

them reaching the epidermis. His figures not only show filaments clearly but indicate that the boundaries of the chambers are distinct, in this respect also differing from Schiffner's account.

The green tissue of *G. fragrans* is so compact that it is difficult to make out its true structure from ordinary hand sections. Even microtome sections are not always easy to interpret, but they give a much clearer idea of the complex arrangement of the cells and of the intricate system of aërating chambers and help to explain some of the conflicting statements in the published descriptions. In a transverse section, such as the one shown in FIG. 1, the cham-

bers are seen to be in three or four layers in the thickened median portion of the thallus. As the margins are approached the thallus becomes thinner, and the number of layers decreases until only the uppermost layer is left. Except in this uppermost layer the chambers are usually polygonal in outline and tend to be isodiametric. In the uppermost layer they tend to be elongated vertically, as shown in the spaces *a* and *b*. That the spaces communicate with one another is also indicated in the figure. The space *c*, for example, is connected with a space nearer the epidermis, and the space *d* probably represents a passageway to a chamber in another section. The figure seems, at first sight, to confirm the statements made by Müller, that both filaments and cell plates are present. Immediately beneath the pore there are apparently three filamentous outgrowths, *e*, *f*, and *g*, and a plate-like outgrowth is clearly shown at *h*. Of course, as Schiffner intimates, apparent filaments may be nothing more than sections of cell plates. In the section drawn careful focusing does indeed show that *e* and *f* are in close contact with another apparent filament in another plane, and the same thing is true of other apparent filaments in the section. Some of the cell plates, moreover, appear to have a fluted surface, so that a section cut parallel with the surface of the plate might readily give the impression of a series of filaments. At the same time there are many apparent filaments which seem to be entirely free from one another, and it is impossible to determine their true status except by the study of other sections. It will be noted that the more deeply situated chambers are free or nearly so from outgrowths of any kind.

The figure is of further interest in showing that some of the apparent filaments and plate-like outgrowths end freely in the chamber without reaching the epidermis, this being especially true in the vicinity of the pores; others, as shown by the one between the spaces *a* and *b*, extend to the very epidermis and seem to be connected with it. It is doubtful, however, if the connection is ever anything more than a close contact, such as the free filaments in *Marchantia* and *Conocephalum* often exhibit. No instance has been observed where an outgrowth extends downward from the epidermis and ends freely in a chamber, and there is no adequate evidence that the epidermal cells themselves ever give

rise to outgrowths, as Schiffner suggests may be the case. The original boundaries of the dorsal air chambers are not absolutely unrecognizable, but they are by no means as distinct as Massalongo's figure represents them. In FIG. 1 the boundaries of the chamber with the air-pore are shown at *i* and *k*, while another boundary is situated at *l*.

The longitudinal section drawn (FIG. 2) brings out the fact that many of the air chambers are more or less elongated. This is strikingly true of those most deeply situated but is also well

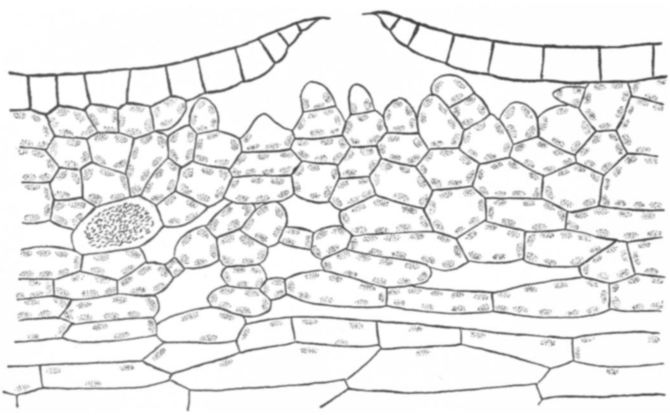


FIG. 2. Longitudinal section through epidermis and green tissue, × 270.

shown by the chamber with the air-pore, although the actual boundaries of this chamber are not definitely indicated. It will be noted that the upper margin of the cell plate represented, which extends almost longitudinally beneath the pore, is distinctly dentate, some of the teeth being over a cell in length. This accords, on the whole, with Schiffner's statement that the marginal cells of the plates may project as teeth. Although some of the teeth shown are more than projecting cells, it would be a stretch of the term to describe them as filaments. The figure, therefore, presents no evidence of the occurrence of true filaments. Other sections, however, show apparent filaments, similar to those represented in FIG. 1.

According to Schiffner, a section through the green tissue parallel with the surface of the thallus will at once show that the chambers are destitute of free filaments. FIG. 3 shows a part of such a

section, cut immediately below the epidermis, and seems at first to belie his statement. The figure shows the partitions, almost complete, of an air chamber, the cells being distinguished by stippling. Only one end of the chamber is represented; the other end did not show because the section was slightly oblique in that region and passed through the epidermis instead of the green tissue beneath. That the stippled cells represent the boundaries of a chamber is evident from their close union and also from the

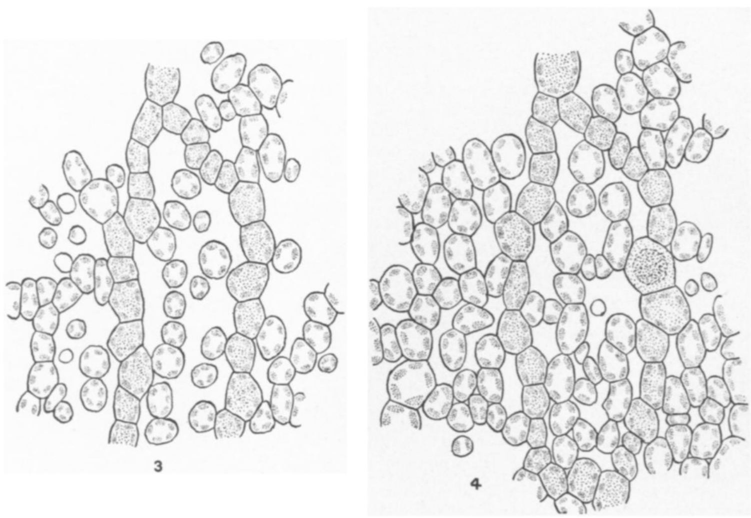


FIG. 3. Section parallel with the surface, just below epidermis, × 270.
FIG. 4. Section a short distance below the one shown in FIG. 3, × 270.

fact that an epidermal pore was situated above the middle of the space which they enclose. It will be seen that the chamber contains a number of cells, circular in section and either entirely free or else loosely connected with one another or with the cells of the partitions. Similar cells are shown elsewhere in the figure, and a superficial examination would interpret them as the sections of filaments, especially if they were considered in connection with FIG. 1.

The incorrectness of this interpretation is brought out by a comparison with FIG. 4, which shows the same chamber at a lower level, the cells of the partitions being again indicated by stippling. In this figure the complete boundaries of the chamber

are shown, but the cells enclosed present a very different appearance. They are not only much more numerous but are, with a few exceptions, more or less firmly united, and the entire chamber is thus divided up into smaller chambers, some of which seem entirely cut off while others show their connections with other chambers. The seven cells shown on the right of the left-hand partition in FIG. 3 are represented in FIG. 4 by seven united cells, showing at once that these seven cells are not the cross sections of filaments but simply the cross sections of teeth, like those shown in FIG. 2. Similar conclusions would be created by comparing other apparently free cells in FIG. 3 with their representatives in FIG. 4. It thus becomes established that there are no free filaments in the chambers. It will be noted further that FIG. 4 presents a much more complicated condition than FIG. 3 and that the boundaries of the air chamber would be hardly distinguishable except through comparison with the simpler figure. It is probable that a section like the one shown in FIG. 4 was responsible for Schiffner's statements, which it certainly strongly supports.

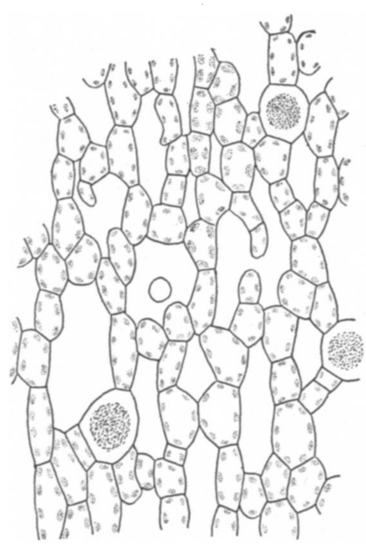


FIG. 5. Section parallel with the surface below the dorsal layer of chambers, × 270.

In FIG. 5 a section from another thallus is shown, cut at a still lower level. This section shows a loose spongy tissue, two of the chambers being connected by a passageway. Cellular outgrowths are very infrequent, but a single cell, apparently free, is shown in one of the chambers, and a single short outgrowth in another. When compared with FIG. 4 the spaces are relatively larger and fewer and the tissue in consequence much less compact. Sections cut farther down show elongated spaces, similar to those represented in FIG. 2, while sections beneath these show the ventral parenchymatous tissue without spaces of any sort.

It is clear from a comparison of transverse, longitudinal and horizontal sections that a distinction may be made between the dorsal layer of air chambers in *Grimaldia* and the more deeply situated layers. In the dorsal layer the original chambers show a secondary partitioning by a system of more or less vertical cell plates, the free margins of which sometimes bear scattered teeth, apparently always less than two cells long. Except for these teeth the chambers lack filaments completely. In the more deeply situated layers, the chambers are much simpler and rarely show evidences of any kind of outgrowth. These conclusions show the incorrectness of certain statements made by Stephani, K. Müller, and Massalongo and the essential correctness of Schiffner's account.

The complex conditions found in the green tissue of *Grimaldia* are duplicated by *Plagiochasma* and by certain species of *Asterella*. The other genera showing the *Reboulia* type of air chamber have a much looser green tissue, the secondary partitioning being less highly developed or absent altogether.

ORIGIN AND ENLARGEMENT OF THE AIR CHAMBERS

The development of the air chambers in the Marchantiales has aroused a good deal of interest among students of the Hepaticae, and the history of the subject is fully given by Barnes and Land (1). The explanation which they advance to account for the origin of the chambers differs in certain respects from the older explanation advanced by Leitgeb and accepted by many of his successors. Leitgeb's explanation was based primarily on his study of *Riccia*, but he extended its application to the more complex genera. According to his ideas the air chambers do not originate in compact tissue, and no splitting of cell walls is involved in their formation. They arise, rather, on the surface of a young thallus and are due to a cessation of upward growth in certain limited areas, the surrounding parts growing upward vigorously. The areas where growth is supposed to cease are situated in most cases where four of the surface cells come together; they mark the lower ends of the chambers, the vertical extent of which depends upon the degree of upward growth which the surrounding parts exhibit.

According to Barnes and Land there is nothing to support Leitgeb's views. In their opinion the chambers always originate in compact tissue below the surface of the young thallus by a splitting of cell-walls and, in case the mature chamber has an epidermal pore, the splitting extends upward until the surface is reached. They based their conclusions on a study of *Ricciella* (*Riccia fluitans* L.), *Ricciocarpus* (*Riccia natans* L.), *Marchantia*, *Lunularia*, *Conocephalum*, *Dumortiera*, *Asterella* (*Fimbriaria*), and *Plagiochasma*, and assumed that they would apply as well to *Riccia* (in its restricted sense). After the chambers are once established their increase in size need not involve any further schizogenous processes. It is largely brought about by the growth of the cells surrounding the chamber, and may be wholly brought about in this way; in other words, by the surface extension of the bounding cell-walls. According to Leitgeb's ideas the increase in the size of the chambers is brought about in much the same way, except that a total absence of splitting is always assumed. It will be seen, therefore, that the most important differences between the two explanations are concerned with the very beginning of the developmental process: according to Leitgeb the chamber is superficial in origin and no splitting occurs; according to Barnes and Land the chamber is not superficial in origin and splitting does occur.

Among recent papers dealing with air chambers, those by Miss Hirsh (4), Pietsch (8), Deutsch (3), Miss O'Keeffe (7) and Miss Black (2) may be briefly noted. Miss Hirsh's work is based largely on *Ricciocarpus natans* (L.) Corda and *Riccia Frostii* Aust. She reaches the conclusion that the first of these species agrees with Barnes and Land's explanation, while the second agrees with Leitgeb's. Her figures of *R. Frostii*, however, by no means support this conclusion fully. Although they show that the chambers drawn may have been superficial in origin, they show as well that a splitting must sometimes have occurred, because some of the chambers extend below the original surface of the thallus. This is brought out clearly by her *f. 6*, upon which she lays especial emphasis. This figure, in fact, presents no convincing evidence that the chamber may not have been initiated by a schizogenous process.

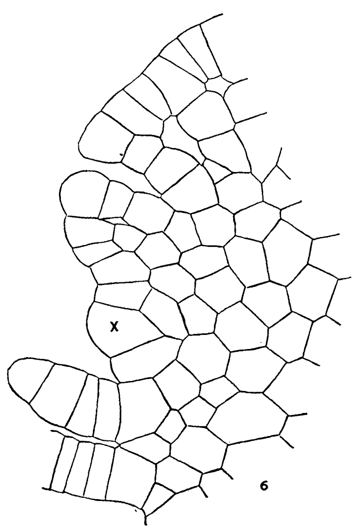
Pietsch's work is remarkable for its thoroughness and accuracy. It deals with species of *Riccia* and *Ricciella*, and his account is therefore based on the group of plants from which Leitgeb drew his conclusions. Although he criticises the work done by Barnes and Land, his observations lead to similar conclusions, so far as the development of the air chambers is concerned. He finds that even in *Riccia* the chambers originate from a splitting of cell walls, the split beginning below the surface and then extending upward until the surface is reached.

Deutsch's paper, devoted to *Targionia hypophylla* L., includes an interesting observation on the development of the air chambers. He states that they arise by a splitting apart of cells close to the apical cell but maintains that the split begins on the outside and extends inward, instead of beginning below the surface and extending outward. The *f. 3*, which he cites as evidence, would be more convincing if the youngest chamber shown did not extend into the hypodermal tissues; as the figure stands it might equally well bear the opposite interpretation from the one drawn. Deutsch does not consider that his account differs in any essential respect from the explanation of Barnes and Land, in spite of the superficial origin which he assigns to the chambers. Miss O'Keeffe, who also worked on *Targionia*, fully supports Deutsch in his statements about the origin of the chambers. Fortunately, the youngest chamber which she shows (*f. 1, A, a*) seems to be conclusive; it appears in longitudinal section as a split between two superficial cells and does not extend beyond them.

Miss Black's paper deals with *Riccia Frostii*, one of the species investigated by Miss Hirsh, and the same conclusions are drawn as to the origin of the air chambers. Her *f. 6*, however, is open to the same criticism as Miss Hirsh's figures. It represents the apical region of a thallus cut longitudinally and including five young air chambers, but even the youngest of these projects below the original surface, showing that a splitting of a cell wall must have taken place. Miss Black emphasizes the fact that she observed no cases in which an intercellular space appeared below the surface and then broke through to the outside, so that her conclusion regarding the superficial origin of the chambers seems justified. At the same time her figure presents no evidence that

the chambers may not have originated from splits between superficial cells, as Deutsch and Miss O'Keeffe maintain is the case in *Targionia.*

The thallus of *Grimaldia fragrans* is so complex that it is impracticable to trace the cell divisions which take place in the segments cut off from the apical cell, as Pietsch has so ably done in the case of *Riccia glauca* L. FIGS. 6–8, however, give some idea of the apical region and bring out the fact that a single apical cell with four cutting faces is present. In FIG. 6, immediately above the apical cell the meristematic tissue forms a compact mass



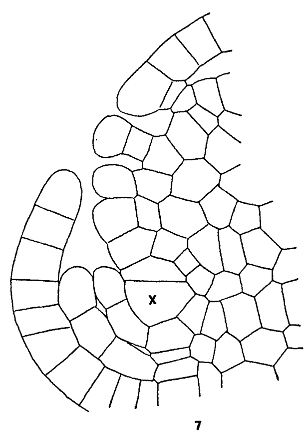


FIG. 6. Longitudinal section through a growing point, × 500. *x*, apical cell.
FIG. 7. Longitudinal section through another growing point, × 500. *x*, apical cell.

without intercellular spaces. Between the fourth and fifth cells the first indication of a chamber appears in the form of a split a short distance below the surface. Between the fifth and sixth cells an older and longer chamber is visible, which has reached the surface, apparently through the upward extension of a similar split. The elongation and widening of the chamber have been largely due, it would appear, to the growth of the bounding cells. The still older chambers shown in the figure are not cut squarely in the middle and need not be further considered.

In FIG. 7, which represents the apical region of another thallus, a somewhat different condition is revealed. In this case the first indication of an air chamber appears between the third and fourth cells and is likewise in the form of a split, but this time the split evidently began on the outside and extended inward. Although the chamber is thus superficial in origin, there is no evidence that a surface area has had its upward growth arrested, as Leitgeb's explanation demands. The split clearly extends inward from the original surface. The chamber between the fourth and fifth cells is considerably deeper and broader, and it is clear that its increase in size has involved further schizogenous processes. The next chamber shown gives evidence of a further horizontal extension.

It would appear from these two figures that the air chambers in *Grimaldia fragrans* owe their origin to a splitting of cell walls, but that the place where the split first makes its appearance is not always the same. It may be below the surface and extend outward, in which case it agrees fully with the explanation advanced by Barnes and Land; it may be at the surface and extend inward, thus agreeing with Deutsch's account of *Targionia hypophylla*. In the writer's opinion the figures published by Miss Hirsh and Miss Black might be interpreted in the same way as FIG. 7, so that there still seems to be no conclusive evidence that Leitgeb's explanation ever applies.

FIGS. 8–10 yield further evidence as to the origin of the chambers; they were all drawn from a single section, cut at right angles to the long axis of the thallus, and show for the most part superficial cells. In FIG. 8 the apical cell appears in the form of a rectangle. Directly above it an air chamber reaching the surface is shown between the fourth and fifth cells, corresponding apparently with the chamber between the fourth and fifth cells of FIG. 7. The schizogenous origin of this chamber seems clear, but there is nothing to show whether the split began at or below the surface. Between the third and fourth cells no signs of a chamber can be discerned, although a superficial split may be present like the one shown in FIG. 7. The figure at any rate gives no evidence of a split beginning below the surface.

FIGS. 9 and 10 are much more conclusive. They represent a

portion of the thallus to the right of the apical cell and derived from lateral segments. In drawing FIG. 9 the microscope was focused on the surface of the cells in a circumscribed area; in drawing FIG. 10 it was focused a little below the surface of the same area. FIG. 9 shows a series of cells in close union and two air chambers which have reached the surface; FIG. 10 shows the same two chambers and six additional ones. The latter clearly represent schizogenous spaces below the surface and demonstrate an origin like that of the youngest chamber in FIG. 6.

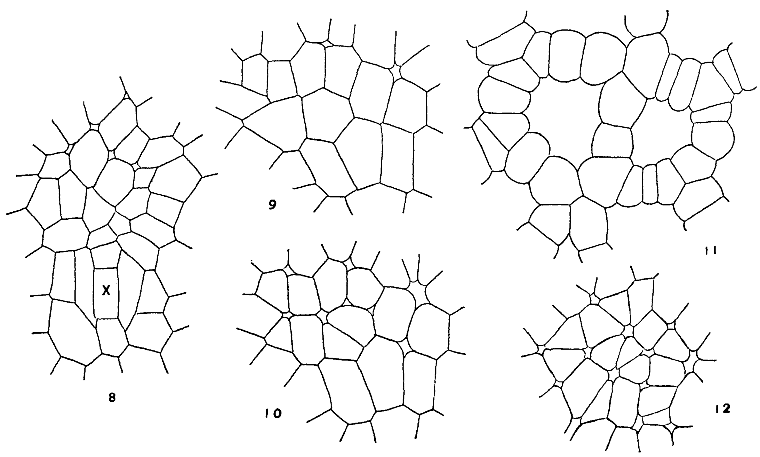


FIG. 8. Transverse section through a growing point, × 500. *x*, apical cell.
FIG. 9. Superficial cells to the right of the apical cell shown in FIG. 8, × 500.
FIG. 10. The same region as that shown in FIG. 9, but at a slightly lower focus, more very young dorsal chambers being visible, × 500.
FIG. 11. Slightly older dorsal chambers than those shown in FIG. 10, the section parallel with the surface, × 500.
FIG. 12. Section just below the one shown in FIG. 11, the numerous intercellular spaces being the beginnings of more deeply situated chambers, × 500.

The rudimentary chambers shown in FIGS. 6–10 represent the beginnings of the complex dorsal chambers shown in FIGS. 1–4. The later stages in the development of these chambers and the origin and development of the more deeply situated chambers are exceedingly difficult to follow. For a while the dorsal chambers are distinct enough in sections cut immediately below the epidermis. Such a section is shown in FIG. 11, where two complete chambers and parts of six others are represented. The increase

in size which these chambers show, when compared with the small intercellular spaces in FIG. 10, is due to the vigorous growth of the bounding cells, accompanied by rapid cell divisions. At this stage the partitions show no evidence of outgrowths. FIG. 12 represents the section just below the one shown in FIG. 11, the cells drawn, in part at least, forming the floors of the dorsal chambers. The figure shows many intercellular spaces, which are clearly schizogenous in origin; these spaces represent the beginnings of the more deeply situated chambers or, in some cases, the passageways leading from these chambers to the dorsal chambers.

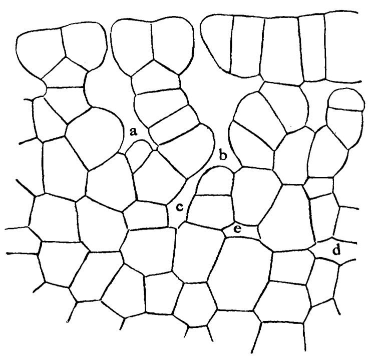


FIG. 13. Longitudinal section through young chambers, × 500. *a–e*, more deeply situated chambers.

A longitudinal section, representing about the same stages as those shown in FIGS. 11 and 12, may be seen in FIG. 13, the left-hand side of the figure being toward the apical cell. The very rapid development of the chambers is clearly indicated, and light is thrown on the way in which the deeper chambers originate, such chambers being indicated by the letters *a–e*. It will be seen that some of these chambers seem to be completely enclosed, showing that they may have originated by a splitting of cell walls in compact tissue, and that others already communicate with more dorsally situated chambers. Whether the connecting passageways are always formed subsequently to the chambers, or whether the formation of the passageways may sometimes precede that of the chambers is not altogether clear. If the older, right-hand side of the figure is compared with the younger, left-hand side, it becomes evident that the tissue with intercellular spaces has almost tripled in thickness and that the dorsal chambers have become distinctly deeper. The rapid growth involved in these changes has taken place in the original partitions of the dorsal chambers, in the cells which formed their irregular floors and in the cells immediately beneath. As the writer conceives the process, the growth of the partitions is both horizontal and

vertical, the growth in the latter direction being often equalled by the upward growth (accompanied by cell division) of the cells forming the floors of the chambers; these in turn remain more or less united with one another and with the cells of the partitions and in this way form the system of united cell-plates in the dorsal chambers. At a later stage the margins of some of the plates which end freely in the chambers give rise to teeth as shown in FIG. 2.

It is difficult to secure direct evidence from the vegetative thallus that the partitions form surface-outgrowths. FIG. 14, however, which is drawn from a section of the young female receptacle, shows that such outgrowths are possible. The section was cut parallel with the upper surface of the receptacle, and the figure shows two complete chambers and parts of eight others; two of the latter contain sections of the tubular epidermal pores which hang down from the roofs of the chambers. The partitions are one cell thick but give the impression of being thicker when cut obliquely. The outgrowths originate as projections of cells which become cut off by walls and then continue their growth and cell-divisions. In the vegetative thallus such outgrowths evidently play a very minor part in the development of the green tissue.

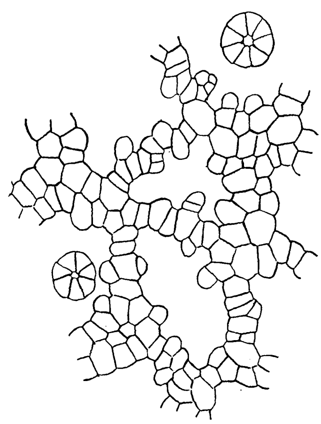


FIG. 14. Section parallel with the surface of a young female receptacle, just below the epidermis, $\times$ 270.

The chambers below the dorsal layer make their appearance very early, as seen in FIGS. 12 and 13, although they always appear later than the dorsal chambers. As the thallus becomes differentiated, these chambers increase rapidly in size through the growth of the bounding cells, but the appearance of new chambers, except in the apical region, has not been demonstrated and seems improbable. If schizogenous processes play a part in the enlargement of these chambers, it is only to a very limited extent.

The green tissue in the thallus of *Plagiochasma* bears a strong

resemblance to that of *Grimaldia*. Its development has been described by Miss Starr (10), her investigation having been based on an undetermined species from Mexico. She confirms the earlier observation of Barnes and Land that the air chambers of *Plagiochasma* owe their origin to a splitting of cell walls below the surface. She notes further that the chambers are at first deep and narrow but that they soon become wide and irregular, and she ascribes the changes in size and form which they show to a "stretching and tearing of tissues between neighboring chambers." In other words she considers that schizogenous processes play a leading part in the enlargement of the chambers as well as in their origin. This conclusion is hardly supported by her *f. 11* or by the earlier figures published by Barnes and Land (1, *f. 17–22*). Although these figures indicate a schizogenous origin of the chambers, they do not disprove that the enlargement is mainly due to the growth of the surrounding cells.

SUMMARY

The air chambers of *Grimaldia fragrans* are in several layers in the thickened median portion of the thallus.

The dorsal chambers communicate with the outside by means of epidermal pores. They are subdivided by an irregular system of more or less vertical, united cell plates, enclosing narrow spaces, so that the boundaries of the chambers are difficult to distinguish. The cell plates sometimes reach the epidermis and sometimes do not; in the latter case the free margins sometimes bear scattered teeth, less than two cells in length, especially in the vicinity of the pores. Except for these teeth the chambers lack filaments completely.

The more deeply situated chambers communicate with one another and with the dorsal chambers by means of passageways; they are scarcely or not at all subdivided by cell plates.

The chambers all owe their origin to a splitting of cell walls in closely united tissue. In the case of the dorsal chambers the split sometimes begins below the surface and extends outward; sometimes at the surface and extends inward.

The dorsal chambers appear first, very close to the apical cell, but the more deeply situated chambers appear soon afterwards.

The increase in the size of the chambers is due largely to the growth of the bounding cells and only slightly to further splittings of cell walls. The system of united cell plates in the dorsal chambers and the partitions between the chambers increase in vertical height simultaneously. Direct outgrowths from the surfaces of cell plates play a very small part in the process of subdivision.

The material upon which this investigation was based was collected and prepared by Mr. John F. Logan, who expected to utilize it in his own studies. Through the pressure of other work his plans could not be realized, and his preparations were placed at the disposal of the writer for examination. The writer would therefore express his sincere thanks to Mr. Logan for his courtesy.

SHEFFIELD SCIENTIFIC SCHOOL,
YALE UNIVERSITY

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